

ORIGINAL ARTICLE

Diversity of leaf litter ant communities in Ton Nga Chang Wildlife Sanctuary and nearby rubber plantations, Songkhla, Southern Thailand

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Abstract

Bickel, T.O. and Watanasit, S.

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Songklanakarin J. Sci. Technol., 2005, 27(5) : 943-955

Large areas of Southern Thailand's former natural rainforest have been replaced by rubber plantations. Despite the fact that rubber plantations dominate the landscape, little is known about its capacity to sustain forest dwelling species. We used leaf litter ants as a bioindicator from two natural forests, a rubber plantation forest and a completely cleared ruderal area in Southern Thailand, Songkla Province. There was a substantial decline in ant diversity from the undisturbed forest towards the ruderal area along a gradient of environmental disturbance. Additionally, there was a turnover in species composition between the different habitats and an increase in arboreal species "enhancing" the sparse ground foraging ant community in the plantation habitat. Also, alien tramp species replaced native species in the plantation and ruderal habitats. This study shows that despite their forest like appearance rubber plantations are a poor habitat for native leaf litter-inhabiting ants and unsuitable to sustain biodiversity in general. The changes in community structure in the secondary forest showed the importance of primary forest habitat to maintain regional biodiversity.

Key words : diversity, ant communities, rubber plantation, tropical rainforest, southern Thailand, leaf litter

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Received, 4 November 2004 Accepted, 21 March 2005

บทคัดย่อ

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ความหลากหลายของสังคมตามซากใบไม้และตามพื้นดิน ในเขตรักษาพันธุ์สัตว์ป่า
โตนงาช้าง และพื้นที่ป่าสวนยางพาราที่อยู่ใกล้เคียง ของจังหวัดสงขลา ภาคใต้ของ
ประเทศไทย

ว. สงขลานครินทร์ วทท. 2548 27(5) : 943-955

พื้นที่ป่าดิบชื้นภาคใต้ของประเทศไทยได้ถูกแทนที่ด้วยสวนยางพารา ทำให้พื้นที่สวนยางพาราเป็นพื้นที่เด่น แต่สิ่งมีชีวิตที่อาศัยอยู่ในพื้นที่สวนยางพารายังมีความรู้ร้น้อยมาก ในการศึกษาครั้งนี้ได้ทำการเปรียบเทียบมดที่อาศัยตามซากใบไม้และตามพื้นดินเป็นดัชนีบ่งชี้ในด้านความหลากหลายในพื้นที่ป่าธรรมชาติสองพื้นที่ พื้นที่ป่าสวนยางพาราและพื้นที่ป่าที่ถูกทำลายอย่างสิ้นเชิงของภาคใต้ประเทศไทยในจังหวัดสงขลา ผลการศึกษาพบว่าการลดลงของความหลากหลายของมดอย่างมากตามความรุนแรงของการถูกรบกวนระหว่างป่าธรรมชาติกับพื้นที่ป่าที่ถูกรบกวน นอกจากนี้ยังมีการเปลี่ยนแปลงองค์ประกอบของชนิดมดระหว่างถิ่นที่อยู่อาศัยที่แตกต่างกันและมีการเพิ่มขึ้นของมดที่อาศัยอยู่ตามต้นไม้ไปหาถิ่นตามพื้นป่าของสวนยางพารา และยังพบว่าชนิดมดที่มาจากแหล่งอาศัยอื่นเข้ามาแทนที่ชนิดมดที่อยู่ดั้งเดิมในป่าสวนยางพาราและพื้นที่ป่าที่ถูกรบกวน การศึกษาครั้งนี้แสดงให้เห็นว่าพื้นที่ป่าสวนยางพาราเป็นพื้นที่ที่ไม่เหมาะสมสำหรับชนิดมดดั้งเดิมที่อาศัยตามซากใบไม้และตามพื้นดิน และไม่เหมาะสมในการที่ทำให้ความหลากหลายชนิดมดอยู่ได้อย่างยั่งยืน การเปลี่ยนแปลงโครงสร้างของชุมชนสิ่งมีชีวิตในป่าพื้นสภาพแสดงให้เห็นถึงความสำคัญของพื้นที่ป่าธรรมชาติที่ทำให้ความหลากหลายของสิ่งมีชีวิตดำรงอยู่ได้

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Tropical lowland rainforests are recognized as the most diverse terrestrial ecosystems that harbor only a roughly estimated number of species (Erwin, 1995; Stork, 1988). The South East Asian region, especially, is known for its species richness (Brühl *et al.*, 1998; Hammond, 1990; Laidlaw, 2000).

Despite their high conservation value, tropical rainforests are vanishing quickly and are heavily used for timber extraction and are being displaced for agricultural purposes including oil palm and rubber plantations.

In Southern Thailand vast areas of natural evergreen rainforest have been cleared for the economically important production of natural rubber that produce an annual income of more than 2 billion US\$ each year (Watanasit, 2003). Primary rainforests are mainly restricted to natural reserves and national parks.

Although the negative influences of logging as a disturbance on forest ecosystems is well

established (Brühl, 2001; Majid and Jusoff, 1987; Uhl and Vierira, 1989; Willot *et al.* 2000) there is still no halt in the destruction of tropical rainforest in the search for valuable timber.

Beside the comparably well studied influences of logging on rainforest communities, there is little known about the communities that persist in forest-like plantation habitats such as the rubber and oil palm plantations that are - from an aerial viewpoint - an important habitat type (Brühl, 2001; Maryati and Chung, 1995). The homogeneous plantation habitats are expected to be of low value to native rainforest dwellers. To test this hypothesis we studied ant communities in natural forests, a nearby rubber plantation and a wasteland area.

Ants were chosen for their suitability as bioindicator species (Alonso, 2000) and their ecological significance in forest ecosystems. Although ants are a less outstanding group in terms of species diversity, they are, beside termites, the

single most important arthropod group alone for their dominance in animal biomass. Ants play important functions in forests ecosystems like the turnover of soil (Gunadi and Verhoef, 1993), and nutrition transport and they actively manipulate their own environment (Jones *et al.*, 1994). Additionally ants have close ties and mutual links to other organisms and their important function as invertebrate predators demonstrates their special role in tropical rainforest.

Material and Methods

Study sites

Ants were collected between 18 and 24 March 2002 in Ton Nga Chang Wildlife Sanctuary (TWS), Southern Thailand. The Reserve is located in the mountainous border area between Songkhla and Satun province approximately 50 km south of Haad Yai (longitude 15° 33' - 16° 23'N, latitude 99° 33' - 99° 7' E) and consists of c. 3000 ha dipterocarp evergreen rainforest. Parts of the park are a popular recreation area. The region around the waterfall near the park entrance is visited by numerous tourists every day. However, few people walk deeper into the forest, therefore the study sites are not disturbed by tourist activities. The climate in this area is influenced by the northeast monsoon with the wettest months from October to December and an annual rainfall of more than 2000 mm (Watanasit *et al.*, 2000).

Four sites characterized by different disturbance regimes through land use (logging, agriculture) were selected within the reserve and in close proximity to it: a primary forest site, located 2 km uphill of the Waterfall area, a secondary forest site near the sanctuary entrance, an old growth rubber plantation of approximately 5 ha in close vicinity to the reserve, and a ruderal area (wasteland) near the reserves management house of 1 ha size. The primary forest site (PF) was characterized by dense under growth, a high proportion of large trees and a closed multi-layered canopy. The secondary forest site (SF) was more open, with multiple gaps in the canopy. Nevertheless, the overall degree of disturbance was low

as the number of large tree species was high and logging must have taken place at least 50 years ago. The rubber plantation (PL) consisted of old grown rubber trees (10-15 m tall) and had no undergrowth. Leaf litter was not existent in contrast to the two forest plots. The canopy was closed but very thin (single layered) permitting sun to reach the ground frequently. The ruderal site (RU) was covered partly by small herbaceous plants (50% of the area), the rest by exposed bare rock/soil.

Sampling in the primary forest site was conducted along the uphill trail between two established primary forest research plots (Watanasit *et al.*, 2000) of TWS. In the secondary forest, sampling was performed behind a secondary forest TWS plot following the trail into the forest interior starting at least 300 m inside the forest. Due to the smaller size of the rubber plantation and the ruderal area sampling took place in the complete area instead of the linear transect design applied in the forest plots.

Sampling and specimen processing

Ants were attracted with tuna baits placed on the forest floor. Sampling started at 09:00 in all sites with the exception of RU where the evening hours were used (17:00-19:00). Tuna in oil is standard bait for ant collection because of its consistent quality and availability (Bestelmeyer *et al.*, 2000). It can attract a wide range of ant species: large ants tend to collect whole tuna flakes whereas small species ingest the fluid (own observation). Small portions of the well-mixed tuna in oil (1/4 teaspoon) were provided on the forest floor. In each of the habitats 20 baits (25 in primary forest) were presented simultaneously along the trail systems with a distance between each other of 10 m. Baits were initially checked 30 min after bait placement, and three more times in 30 minute intervals. At each bait inspection the number of individual ants was recorded and specimens were collected for later species identification. Specimens were stored in 70% ethanol in individual vials provided with a unique identification code for proper sample identification.

In the laboratory of the Prince of Songkla

University, ant specimens were mounted on cardboard triangles after the convention of Bolton and identified to genus level under a dissecting microscope (Bolton, 1994). Subsequently morphospecies were designated relying on distinctive morphological characters of the worker class (Lattke, 2000). Specimens of the Genus of *Pheidole* were sorted to species level with the key of Eguchi if possible (Eguchi, 2001). Several specimens were compared with the ant collection at Kasetsart University, Forestry Department, Bangkok, for species identification.

Statistical analysis

Data analysis was separated into a numerical species richness analysis and a community comparison between the habitats.

In the numerical analysis of species richness only 'true' leaf litter dwelling species were included in the analysis. Species that typically forage and nest in the lower vegetation or canopy - occasionally observed at baits - were therefore excluded. These comprise species of the genera *Camponotus*, *Oecophylla*, *Tetraponera*, *Polyrhachis* and *Tetraponera*. The reason for the exclusion of these species is their sporadic occurrence on the forest floor and arboreal nesting habits that disqualify them ecologically as leaf litter inhabitants. Additionally these species are collected infrequently for their primarily arboreal life, therefore appearing to be rare (Brühl, 2001), resulting in an overestimation of species richness with richness estimators as these rely partly on the number of rare species in samples. In reality these species can be abundant in the vegetation although they are seldom found on the forest floor. In the community comparisons the vegetation species have been taken into account in some parts (where noted) as they can replace a high proportion of the ground ant fauna in disturbed and non-forested habitats.

For the statistical analysis the data were entered into a matrix in the form of presence-absence data. That is, species were recorded as present in a sample or not. The number of individuals of a species at the baits (abundance

data) was ignored as a high number of individuals of one ant species in a sample could be biased by the proximity of their nest (Maryati and Chung 1995). This approach is often preferred (Brühl, 2001, Longino, 2000) to take into account the high state of aggregation of the eusocial ants leading to a wrong impression of abundance. Consequently, pseudo-abundances were calculated as abundance measurements, that is the summed presence of species in samples of habitats. An abundant species is therefore found in many samples, a rare one in few.

Species richness and diversity

To obtain a measurement of sampling success, species richness in the habitats was estimated using the species richness estimators included in the EstimateS software (Colwell, 1997). The process of species richness estimation is explained in detail in the literature (Brühl, 2001; Colwell, 1997; Colwell and Coddington, 1994, Longino 2000) so its calculation is not discussed here. In this study several species richness estimators were used: Jack1 and 2 (first and second order Jackknife), Chao2, ICE (Incidence based Cover Estimator), MMM (Michaelis Menten Mean) and a Bootstrap estimator. As there is no ideal estimator identified in the literature, the mean of the estimators was calculated to compare the different habitats (Soberon and Llorente, 1993). To measure sample efficiency the proportion of observed species from mean estimated species was calculated.

To determine species diversity within habitats (alpha diversity) the Renyi diversity ordering was performed using the Species Diversity and Richness 2.3 Software (Henderson and Seaby, 1998). To rank the alpha diversity measurements of the communities the Renyi index $H(\alpha)$ was calculated for a range of diversity measurements (including Shannon Wiener's and Simpson's D diversity indices) of the scale parameter α (Legendre and Legendre, 1998). The $H(\alpha)$ diversity was plotted against the scale parameter and the resulting curves were compared. If $H(\alpha)$ values are higher over the full range of α and curves do

not cross, a community is ranked as more diverse.

Species diversity within a region resulting from species turnover between habitats is termed beta diversity. To account for differences in the overall species abundance between the habitats, abundances were divided by the maximum abundance value reached for that species in any one of the habitats prior to any further analysis. Species turnover between habitats was analyzed calculating the widely used 'Sorensen' (Bray-Curtis) distance. Based on these distance measurements a cluster analysis was performed using the UPGMA (Unweighted Pair Group Average) cluster algorithm to analyze community similarities (Krebs, 1989).

Cluster analysis was performed with the PC-ORD program (McCune and Mefford 1999).

Results

Overall taxonomic composition

Overall 28 genera comprising 59 ant species

from 5 subfamilies were recorded in this study from the 85 tuna baits applied in four habitats. For the numerical species richness analysis, 10 assumed tree dwelling/nesting species out of four genera were excluded from further statistical evaluation (see material and methods): *Camponotus* (Formicinae - 2 species), *Oecophylla smaragdina* (Formicinae), *Polyrhachis* (Formicinae - 6 species) and *Tetraponera* (Pseudomyrmicinae 1 species).

More than 50% of the remaining 49 leaf litter species were from the subfamily Myrmicinae (Table 1). Ponerinae and Formicinae were the next most species rich subfamilies. Dolichoderinae and Cerapachyinae accounted only for about 10%.

Species richness estimators and sample efficiency

The largest number of species (S_{obs} = Species Observed) was detected in the primary forest (PF). The number of species gradually decreased towards the wasteland (RU, Table 2). Species richness was

Table 1. Distribution of genera and species numbers of the leaf litter ant community in the different subfamilies. Proportions in % are given in brackets.

Subfamily	Genera	Species
Myrmicinae	10 (40)	27 (55.1)
Ponerinae	7 (28)	9 (18.4)
Formicinae	6 (24)	8 (16.3)
Dolichoderinae	1 (4)	4 (8.2)
Cerapachyinae	1 (4)	1 (2.0)
Total	25	49

Table 2. Recorded (S_{obs} = Species observed) and expected number of species as calculated with different species richness estimators. The sampling success given as proportion of sampled species (S_{obs}) to the estimated species numbers are given in brackets. Maximum and minimum success are indicated by bold numbers.

	Samples	S_{obs}	ICE	Chao2	Jack1	Jack2	Bootstrap	MMMean	Mean
PF	25	26	41 (63.4)	40 (65.0)	38 (67.6)	45 (57.6)	32 (82.4)	47 (54.8)	41 (64.1)
SF	20	23	44 (52.3)	43 (53.5)	36 (63.4)	45 (51.5)	29 (80.2)	48 (48.0)	41 (56.5)
PL	20	16	20 (80.0)	19 (84.2)	21 (77.1)	22 (73.3)	18 (87.1)	22 (73.6)	20 (78.6)
RU	20	8	14 (57.1)	16 (50.0)	12 (67.8)	15 (51.9)	9 (84.7)	9 (92.9)	12 (64.1)

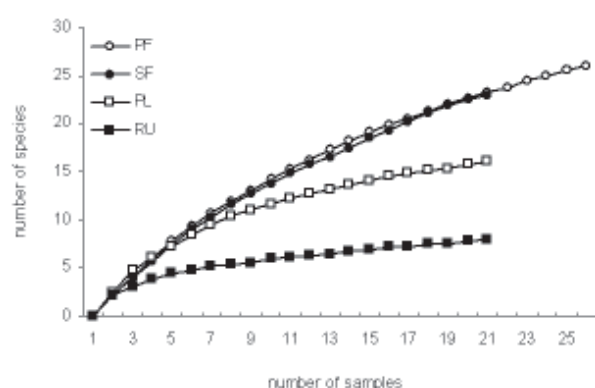


Figure 1. Randomized (100 runs) species accumulation curves of the four habitat types (PF = primary forest, SF = secondary forest, PL = plantation, RU = ruderal area).

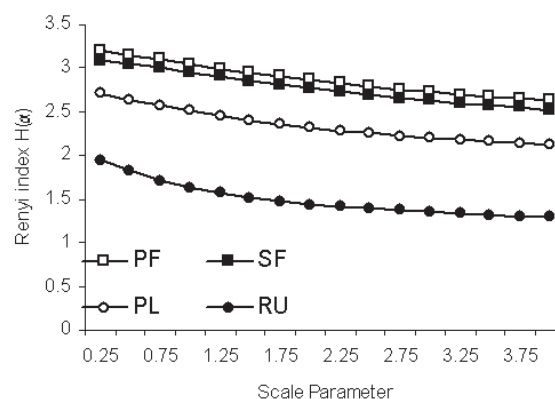


Figure 2. Renyi index $H(\alpha)$ of the different plots along the scale parameter.

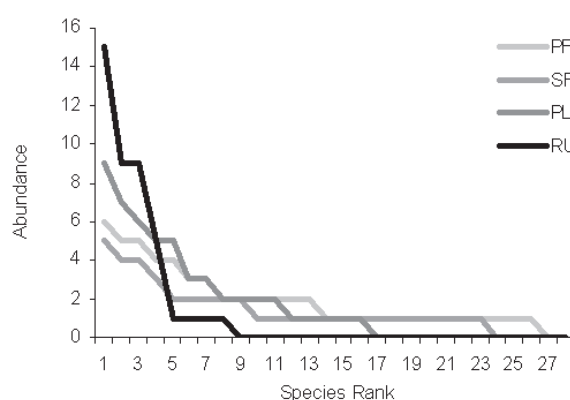


Figure 3. Species rank abundance distribution plot for the four habitats.

estimated with six different species richness estimators. For an easier comparison between plots the mean estimated species number was calculated. With an average of 41 estimated species in the primary and secondary forest, species richness was higher in the two forest plots compared to the plantation with an average of 20 species and the wasteland area with 12 species (Table 2).

As measurement of sample efficiency the number of species of sampled ants (S_{obs}) as a proportion of the estimated number of species was calculated for each estimator (Table 2). Sample efficiency was mostly between 50 and 80% for all

estimators. The highest estimated success for any single estimator was found in the ruderal area (MMMean estimator) with a success of 92.9%, the lowest in the secondary forest baiting with 48%. The mean sampling success was between 56.5% for the secondary forest bait experiment and 78.6% in the rubber plantation.

Randomized (100 runs) species accumulation curves were calculated for each individual plot (Figure 1). The curves of the primary and secondary habitat showed a similar slope and species saturation plateau and were situated above the disturbed area curves. The incline of the rubber

plantation curve is similar to that of the forested areas at the beginning - indicating a high species turnover at the baits - but then flattens. In the ruderal area virtually all species were sampled after a few baits. The increase of new species in the last five baits was 2-3 species in the forested areas and about one species in the two non-forested plots (PL, RU)

Species (α) diversity

With the Renyi index $H(\alpha)$ calculated over the scale parameter α the habitats could be ranked according to their community diversity (Figure 2). Since the lines never cross all habitats are comparable. The primary forest curve was situated slightly above the secondary forest curve ranking the primary forest community as that with highest species diversity. Rubber plantation habitat showed intermediate diversity and the ruderal area the lowest.

Distribution patterns of species in the forests - rare and abundant species

To analyze species distribution in the habitats a rank abundance plot was produced (Figure 3). Species were ranked according to their pseudo abundances (see materials and methods), therefore common species are displayed on the left, the rare ones on the right. The ruderal area was characterized by a small number of species that were very common and a small number of species that were rare placing the curve above all other curves at the beginning but then decreasing rapidly. The plots for primary and secondary forest were different with the most abundant species reaching not half the abundances of the ruderal habitat. However, they do show a high number of rare species extending the curves to the right and with a more linear like appearance. The plantation curve was intermediate between the forest and wasteland curve.

The most abundant species in all habitats were selected to analyze community composition. To account for differences in sample size the proportion of species in samples was calculated (percentage of baits where the species occurred in

the habitat). Some species added to the table were not counted in the species richness calculations as they are assumed to be tree dwelling species (denoted with an *). Species were broadly split into: generalist species (abundant in all habitats) and specialist species (restricted to special habitat types) according to their habitat preference (Table 3). It must be emphasized that specialist means here habitat specialist, not a specialization into ecological niches such as food.

There are two generalist species that were found in high numbers at all baits: *Odontoponera denticulata* and *Tapinoma a.* Additionally we found some generalist species that are common in tree bearing habitats (forest and plantation). These are common *Pheidole* species and the two tree nesting species *Oecophylla smaragdina* and *Tetraponera a.*

Specialist species were sorted based on a disturbance gradient from low disturbance in the primary and secondary forest to high disturbance in the ruderal area. The forest specialist species pool concludes a mix of different genera (mainly Myrmicinae) that are found in the two forest habitat types. Two of the three plantation specialist species are supposed tree nesters (*Camponotus a.*, *Polyrhachis a.*). The tramp species *Anoplolepis gracillipes* was restricted to the plantation and ruderal area. *Pheidologeton diversus* was the only species that was very common in the ruderal area but not found anywhere else.

Besides the change in community composition from un- to highly disturbed habitats there is a further trend for an increase in abundance from the primary forest habitat to the ruderal area. Species tended to be much more dominant at baits in the disturbed habitats and were recorded on up to 75% of the baits.

When the number of species was compared with the number of specialist species (species that occur exclusively in one habitat) it was recognizable that there is a higher proportion of specialist species found in the disturbed habitats. This finding is contrary to the fact that the total species number is much lower here than in the forest habitats (Table 4). Whereas in the primary forest

Table 3. Distribution of abundant species (percentage of sample occurrence) in the habitats, tree dwelling species are denoted with an *, tramp/invasive species with an #.

Ant species	PF	SF	PL	RU	Preferred habitat
<i>Odontoponera denticulate</i>	20	20	45	45	Generalist species - all habitats
<i>Tapinoma a</i>	4	5	35	75	
<i>Pheidole cariniceps</i>	24	10	25	-	Generalist species - only tree bearing habitats
<i>Pheidole hortensis</i>	8	5	30	-	
<i>Tetraponera a*</i>	-	5	20	-	
<i>Oecophylla smaragdina*</i>	-	10	20	-	
<i>Pheidole planifrons</i>	20	15	-	-	Primary and secondary forest specialists
<i>Pheidole longipes</i>	16	25	-	-	
<i>Crematogaster a</i>	16	10	-	-	
<i>Lophomyrmex a</i>	4	10	-	-	
<i>Paratrechina a</i>	8	10	-	-	
<i>Technomyrmex a</i>	4	20	-	-	
<i>Polyrhachis a*</i>	-	-	20	-	Plantation specialists
<i>Camponotus a*</i>	-	-	45	-	
<i>Cardiocondyla nuda#</i>	-	-	25	-	
<i>Anoplolepis gracillipes#</i>	-	-	10	45	Disturbed habitat specialist
<i>Pheidologeton diversus</i>	-	-	-	25	Ruderal specialist

Disturbance
high low**Table 4. Number and proportion of species that are restricted to one habitat.**

	PF	SF	PL	RU
Number of species	26	23	16	8
Unique species	10	8	8	4
Proportion	0.38	0.35	0.50	0.50

habitat 38% of the species are unique to this habitat, more than 50% of the species discovered in the plantation and ruderal habitat are found exclusively here.

Species turnover between habitats

To visualize differences in community turnover between the habitats, a cluster analysis was performed. For cluster analysis the UPGMA (Unweighted Pair Group Average) algorithm was used to group habitats according to 'Sorensen' (Bray-Curtis) distances. In the resulting tree

diagram the ruderal area and the plantation ant communities form a single cluster distinct from the forest plots although similarity between this two is low (Figure 4). The two forest habitats grouped together in a second cluster.

Community composition

To analyze for differences in the community composition between habitats the number of species in different subfamilies was compared (Figure 5). In all habitats the Myrmicinae was the species richest subfamily but there is a considerable drop

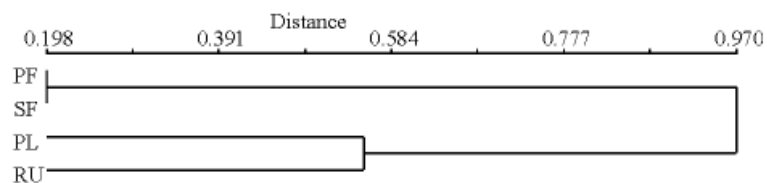


Figure 4. Cluster analysis based on the Bray-Curtis index using the UPGMA cluster algorithm.

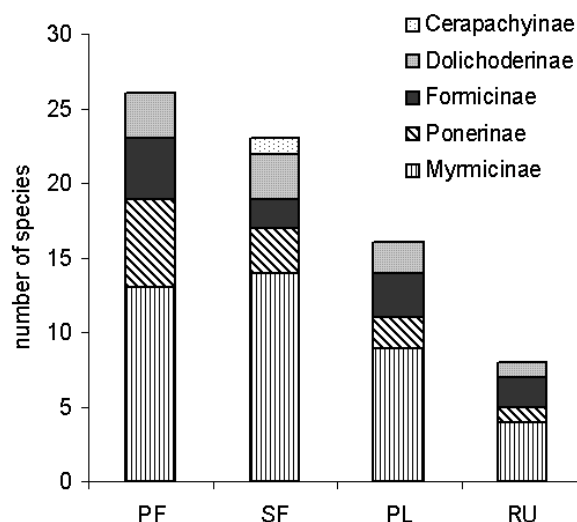


Figure 5. Number of species from the subfamilies.

in species numbers from the natural forests towards the plantation and ruderal habitat. Ponerinae was the second largest subfamily in the primary forest but numbers declined recognizable already in the secondary forest and in the other habitats. Contrary to this, the Formicinae species numbers did not fluctuate between habitats - as did Dolichoderinae species - even in the degraded habitats.

Discussion

The overall species number (59 species) was comparable to two other studies (59 and 35 species) carried out in this region (Watanasit, 2003; Watanasit *et al.*, 2000). The high proportion of Myrmicinae species that typically comprise the bulk of the cryptic species found in South East Asian leaf litter ant communities (Bolton, 1996; Brühl *et al.*, 1998; Ward, 2000) can be seen as an indication that the community was sampled

evenly. There was no obvious bias against larger, more conspicuous, species observable in this study as the baiting method implies (Bestelmeyer *et al.*, 2000). This indicates that although collected species numbers were low the overall pattern of the ant community was not influenced noticeably by sample size or the method, a prerequisite for a valid comparison of the habitats.

Tuna baiting is generally not recognized as the method of choice to sample a large proportion of the species community (Delabie *et al.*, 2000). However, this method is less demanding in terms of materials and costs in comparison to more equipment-intensive methods like litter sieving. Sampling success by baiting is possible only by making multiple observations of baits as there is a considerable temporal turnover at individual baits. Therefore, the usual single collection of specimens at the end of the sampling will only yield a fraction of the species occurring at the baits

over time (personal observation). Although the ant community was sampled only in the dry season the authors are confident that the patterns found are not influenced by seasonality but reflect differences in habitat structure. In a similar study on the ground ant fauna of Sabah no effects of seasonality on ant community patterns in forests with different degrees of disturbance were detected (Brühl, 2001).

Species richness, sampling success and alpha diversity

The actual number of species collected (species observed, S_{obs}) is the most direct measurement of species diversity of a community. The results show that there is a gradual decline of species diversity from the primary forest with the highest species numbers to the species depleted ruderal area. The species-poor rubber plantation reached only 61% and the ruderal area only 31% of the species numbers of the primary forest habitat.

Mean species richness estimations reached a similar level of species richness in primary and secondary forest and a considerably lower one in the non-forest habitats. Mean sampling success - calculated as the proportion of observed species from estimated species richness - was between 56.5 and 78.6%. Performance of most of the estimators was in the same range between 50 and 75% sampling success, with the exception of the MMMean estimator that delivered the highest as well as the lowest efficiency values. Therefore, the mean efficiency values have to be considered as relatively conservative estimates.

Randomized species accumulation curves were saturated for the plantation and ruderal habitats. Although a real asymptotic plateau was not reached for the two forest habitats, the relatively minor increase in species over the last five baits showed that there would be no dramatic increase in species number with further sampling effort. A comparison between habitats should therefore not be influenced by sampling. Additionally, the results suggest that 20 samples would be a minimum number as a compromise between

sampling effort and the aim to collect an ant community as complete as possible for a habitat comparison. This is in agreement with the recommendations given in the standard protocol (ALL) for collecting a ground ant community (Agosti and Alonso, 2000). The comparison of curves produced with the Renyi family ordering revealed highest species diversity along the whole scale parameter in the primary forest and lowest in the ruderal habitat. Since the curves do not cross all habitats are comparable. This was consistent with the findings on species richness and species numbers.

Species distribution and community turnover

Besides a change in species numbers there was a considerable change in the abundance patterns of species in the habitats as indicated by the rank abundance plots. The forest habitats are characterized by a species rich community with low abundance, the plantation and wasteland habitats by a low number of species that are highly abundant. Moreover, there was considerable species turnover between habitats. A cluster analysis revealed distinct communities in all four habitats, the two forest habitats being the most similar.

The analysis of habitat generalists and specialists shows several patterns: 1) there is only a small set of species that can successfully inhabit all four habitats 2) the typical cryptic Myrmicinae species (*Pheidole*, *Lophomyrmex*, *Technomyrmex*, *Paratrechina*) are restricted to the two natural forests and 3) there is a special set of species that were either tree dwelling (*Camponotus*, *Polyrhachis*, *Tetraponera*) or tramp species (*Cardiocondyla*, *Anoplolepis*) which were found in the degraded habitats and 4) there is an increase in the abundance of the species with an increase in disturbance.

That there is a completely different ant community in the disturbed habitats is corroborated by the fact that there is a high proportion of species limited to these habitats. Although species numbers are low, a large proportion is found only there. The change in the community composition was also found on the level of subfamilies. There was

a general decline in the number of Myrmicinae and Ponerinae species whereas the number of Formicinae and Dolichoderinae was constant over all habitats.

Ponerinae species are known to be susceptible to microclimatic changes (Hölldobler and Wilson, 1990) and most Myrmicinae species are characterized as the typical leaf litter inhabitants. Formicinae are mostly tree dwelling species (Brühl *et al.*, 1998) that seemed to replace the leaf litter fauna found in the forest interior. Dolichoderinae are often aggressive species that inhabit large colonies and dominate communities in disturbed habitats (Andersen, 1995).

The drastic change in the ground ant communities in the plantation compared to the forests was apparent from the loss in species numbers as well as the species composition. Ants are known to react to microclimatic conditions and are successfully used as bioindicator species (Andersen, 1993; Andersen *et al.*, 1997; Majer, 1983). A functioning ground ant community was not present in the plantations. Although species numbers were higher than in the wasteland area, probably the result of the less harsh microclimate there, a high proportion of the species there were typical tree dwellers. Important ecological functions like nutrient flows and the turnover of soil, typically performed by ants in the native forests, are likely to be disrupted and not accomplished by tree nesting species.

The species poor ant community in the plantation is notable because it was located in the vicinity of forested areas (less than 1 km). Recolonisation should therefore have been possible after the canopy closed and climatic conditions improved in comparison to the situation right after logging.

The results therefore clearly suggest that rubber plantation forests are in no way an equivalent habitat to natural forests. The natural ground foraging ant community is replaced by tree dwelling species and alien invaders. These invading species are known to have a negative influence on arthropod communities (Green *et al.*, 1999; Hill *et al.*, 2003) and are typical for disturbed plantation habitats (Maryati and Chung, 1995; Baker, 1976).

From a conservation viewpoint, it is becoming clear that protection of biodiversity is only possible in natural forests. Artificial plantation forests are completely unsuitable for most forest dwelling species. Forest reserves are clearly the best way to conserve species. Further spread of plantation forests would lead to further reduction of biodiversity in the region.

Acknowledgements

Thanks are due to Decha Wiwatwitaya for the possibility to use the ant collection at Kasetsart University. Also thanks to Nawee 'Tiger' and Surachai for help with the identification of ants.

Special appreciation to the staff of Ton Nga Chang Wildlife Sanctuary for permission to work in the forest and all the hospitality while we were staying there. Also a 'thank you' for all the help of numerous students at Prince of Songkla and Kasetsart University.

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